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# Eat and be eaten: trophic interactions of the introduced frog *Scinax quinquefasciatus* in anthropogenic environments in Galápagos

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## Abstract

While the Galápagos Archipelago is known for its endemic flora and fauna, many introduced species have also become naturalised there, especially on the human-inhabited islands. The only amphibian species known to have established on the islands, the Fowler's snouted treefrog (*Scinax quinquefasciatus*), is thought to have arrived about two decades ago. Since then, this treefrog has substantially extended its range to the islands of Santa Cruz and Isabela. Our study explores the potential influence of this introduced amphibian on native trophic systems on Santa Cruz and identifies potential antagonists likely to control larval frog populations. To understand the impact of *S. quinquefasciatus* as a predator of local invertebrate fauna, we performed a stomach-content analysis of 228 preserved adult specimens from seven different localities on Santa Cruz. Of the 11 macroinvertebrate orders recorded, Lepidoptera constituted more than 60% of the contents. We also identified active predators of *S. quinquefasciatus* tadpoles: larvae of the endemic diving

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beetle (*Thermonectus basillarus galapagoensis*). To determine the efficiency of this predator, we conducted predator-prey experiments in ex situ conditions. Tadpole predation was highest after first exposure to the predator and significantly decreased over time. Our experimental results demonstrate that although *T. b. galapagoensis* larvae are effective tadpole predators, their feeding saturation rates are likely inadequate for frog population control. Our findings provide the first baseline data necessary to make informed ecological impact assessments and monitoring schemes on Santa Cruz for this introduced treefrog.

**Keywords**
amphibia, Galápagos, introduced species, island biodiversity, predator-prey interactions

## Introduction

Introduced species, which often transition to invasive species, are considered to be a major threat to global biodiversity (Early et al. 2016). The negative impacts of invasive species on native biota are particularly severe in insular ecosystems with high influxes of human trade and travel (Courchamp et al. 2003), such as the Hawaiian Archipelago (Beard and Pitt 2006), Guam (Christy et al. 2007) and Taiwan (Jang-Liaw and Chou 2015). The Galápagos Archipelago is no exception, with over 1500 established introduced species, many of which are invasive (Toral-Granda et al. 2017). Worldwide, frogs represent the highest proportion of the 322 herpetological reported invasions (Kraus 2009). However, apart from a few well-known examples, such as the cane toad (*Rhinella marina*) or the American bullfrog (*Lithobates catesbeianus*) (e.g. Laufer et al. 2008; Measey et al. 2016; Kosmala et al. 2017), amphibian invasions and their impacts on native biota are not well studied. Fowler's snouted treefrog, *Scinax quinquefasciatus* (Fowler 1913), represents one of these cases. Basic data on this species are still lacking, despite its comparatively long introduction history (Cisneros-Heredia 2018): *S. quinquefasciatus* is assumed to have been introduced to Galápagos in the late 1990s (Snell et al. 1999).

Of the four human-inhabited islands of the Archipelago, *S. quinquefasciatus* is only known to occur on Santa Cruz and Isabela. It was formerly also present on San Cristóbal (Cisneros-Heredia 2018), but this could not be confirmed in a recent assessment (Ernst et al. unpubl. data) and breeding populations have never been reported on the island.

Pazmiño (2011) reported a close genetic relationship between the population on Isabela and several populations in the lowlands of western Ecuador (north of Guayas, south of the Manabí and Los Rios Provinces). At least two independent colonisation events took place on the islands (Pazmiño 2011); further investigations of these introduction events are currently underway (Ernst et al. in prep).

The ecology and potential impact of *S. quinquefasciatus* on the native ecosystems of Isabela have previously been addressed in Zurita (2004), Vintimilla (2005) and Mieles (2006). No information of this kind currently exists for Santa Cruz, which has recently experienced agricultural intensification and rapid urbanisation of rural areas

(CGREG 2016). These land-use changes have resulted in the expansion of irrigation systems, including water reservoirs that now provide large permanent freshwater habitats. Since these human developments are likely facilitating the successful establishment and spread of *S. quinquefasciatus* on Santa Cruz, there is an urgent need to study the impacts of this species on the resident fauna.

Invasive species often disrupt predator-prey interactions: as a new predator that consumes native prey (Krisp and Maier 2005), as a new prey item for native predators (Petrie and Knapton 1999; Bulté and Blouin-Demers 2008) or both (Holway et al. 2002). Here, we address both sides of this trophic relationship by (1) determining and quantifying the dietary preferences of adult *S. quinquefasciatus* via stomach-content analysis and (2) identifying potential native tadpole predators and quantifying their predation capacity in controlled ex situ experiments.

## Methods

### Study Area

Our study was conducted in the highlands of Santa Cruz, located at the centre of the Galápagos Archipelago (Fig. 1). The first settlers arrived in the highlands between 1910 and 1938 (Lundh 1995, 1996), subsisting on agriculture and fishing. Over time, the human population grew and spread due to fishing and tourism (Epler 2007). Population growth, combined with the associated plant invasions, led to the degradation of approximately 86% of the highland ecosystems (Trueman et al. 2013).

The highlands of Santa Cruz support greater biodiversity and thus productivity than the lowlands, which are more extensive, but drier (Porter 1984). The annual mean climatic values for the study sites in the highlands of Santa Cruz for the years 1987 to 2019 were: 1380 mm for precipitation, 22.2 °C for temperature and 90.3% for relative humidity (Charles Darwin Foundation, unpubl. data). However, the means for these parameters can vary considerably from year to year, due to the El Niño-Southern Oscillation (ENSO) phenomenon (Snell and Rea 1999).

This study was conducted from April to May 2017–during the rainy season-at one ranch and six agricultural sites in the highlands of Santa Cruz (Fig. 1). Our core site, Rancho El Manzanillo, is located 3 km off the main road that connects the airport ferry port with the town of Puerto Ayora. This traditionally agricultural ranch has recently become a popular ecotourism destination for spotting wild giant tortoises (*Chelonoidis porteri*) in their natural habitat. In the late 1990s, landowners created several artificial ponds to attract tortoises; these water sources now also provide reproductive habitats for *S. quinquefasciatus*. We collected adult frogs and predatory beetle larvae within or near water features at Rancho El Manzanillo (hereafter 'core locality') and six similar agricultural sites (B, C, D, E, F, G; Fig. 1). We conducted the predatory capacity experiments at the core locality.

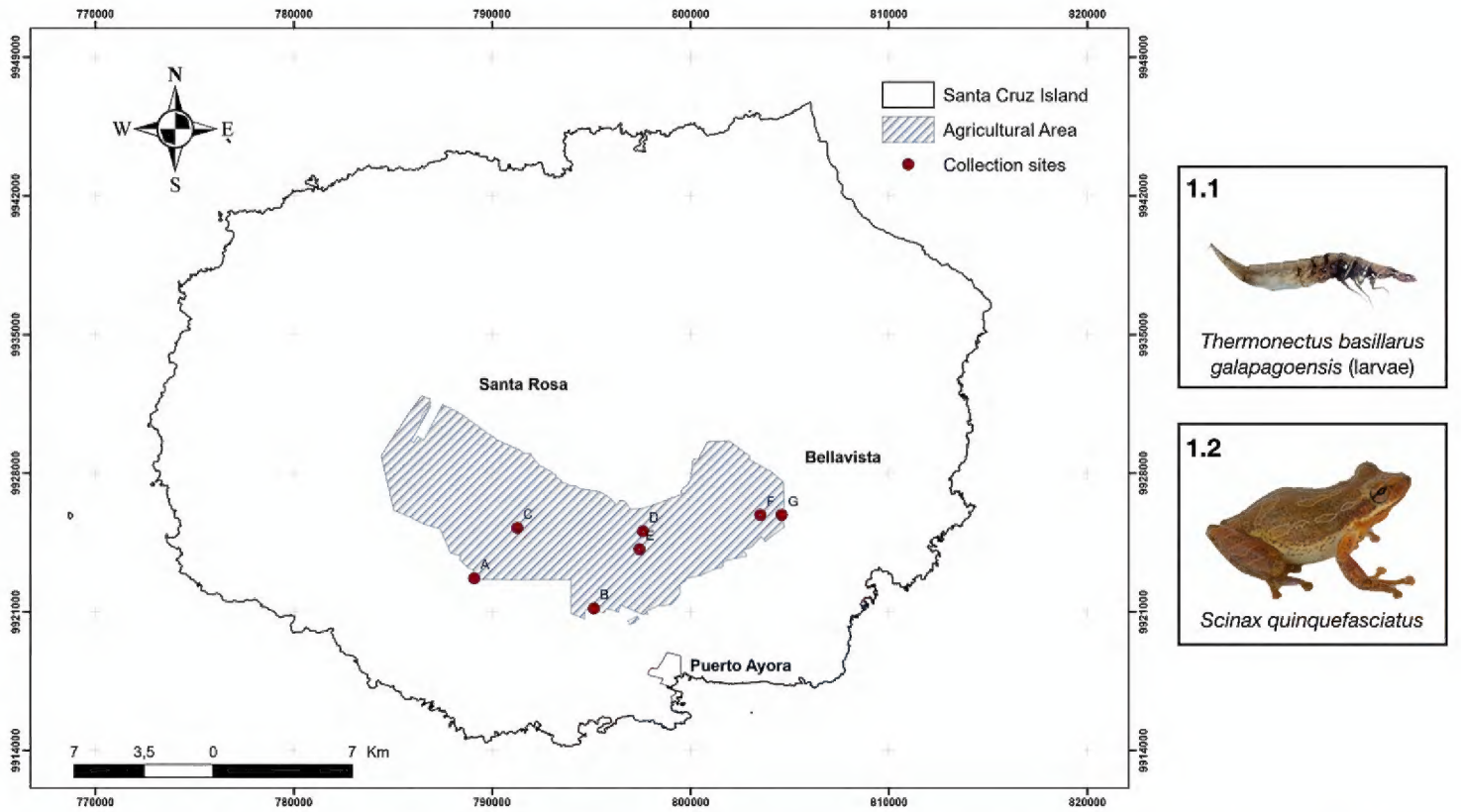


**Figure 1.** Study area and collection sites (red dots) of *Scinax quinquefasciatus* specimens in the highlands of Santa Cruz, Galápagos, Ecuador. A = Rancho El Manzanillo (core locality). B – G = additional collection sites within the agricultural area (grey shading) of the island. 1.1) Larvae of the endemic diving beetle *Thermonectus basillarus galapagoensis*. 1.2) Adult of the introduced frog *Scinax quinquefasciatus*. Not to scale.

### Stomach-content analyses

We captured adult and sub-adult individuals of *S. quinquefasciatus* using Visual (VES) and Acoustic Encounter Surveys (AES), as described by Rödel and Ernst (2004), from 8 pm to 12 am, for 14 consecutive nights. All frogs were euthanised with liquid lidocaine and fixed in 70% ethanol no more than five hours after capture. Samples were then transported to the Charles Darwin Research Station (CDRS), where their digestive tracts were removed following procedures described in Döring et al. (2016). Prey items were examined under an Olympus Stereo Microscope SZ61-RT and identified to order, using reference material from the Terrestrial Invertebrate Collection of the CDRS (ICCDRS 2020). We examined the stomach and intestine content of 228 frogs, 156 from the core locality and 72 from the six other agricultural sites.

### Predatory capacity experiments

For five consecutive days, we surveyed potential larval habitats, including seasonal and artificial ponds, for the presence of tadpoles and their potential aquatic predators. While we observed Anisoptera (dragonfly) larvae-known to be effective tadpole predators elsewhere-in some water bodies, they never co-occurred with *S. quinquefasciatus* tadpoles. Since we only observed the endemic diving beetle *Thermonectus basillarus galapagoensis* in the same water bodies, we chose this species as the target organism for the following predation experiments.

In order to (1) ensure that tadpole exposure to beetle predators was novel and (2) minimise ontogenetic and interpopulation differences in larval predation response (Narayan et al. 2013), we reared the tadpoles used in our experiments rather than collecting them from available ponds. To do so, we first captured four amplectant *S. quinquefasciatus* couples at the core locality and kept them in plastic containers with 100 ml of mixed water (75% rainwater and 25% pond water). After the females had spawned, eggs were transferred to different plastic containers with 200 ml of mixed water. Hatched tadpoles were used in experiments after they reached Gosner stages 21–25 (Gosner 1960). From two different ponds at the core locality, we captured 28 *T. b. galapagoensis* beetle larvae (mean length: 1.59 ± 0.18 cm) with a strainer. Larvae were transferred to plastic containers with 200 ml of mixed water prior to the experiment. In order to equalise their feeding motivation, we fed beetle larvae with two tadpoles from our hatchery every four hours for 24 hours and then deprived them of food for another 24 hours prior to experimentation. To prevent predation events from external predators, all plastic containers were covered prior and during experimentation.

Our experiments consisted of one treatment (predatory capacity) and two survival control experiments (tadpole survival and beetle larvae survival). For the predatory capacity experiments (N = 14), we introduced one food-deprived beetle larva into a plastic container with 20 tadpoles from our hatchery. For the tadpole survival experiments (N = 14), we transferred 20 tadpoles into one plastic container under the same conditions as the previous treatment, but without beetle larva. Finally, for the beetle survival experiments (N = 14), we added one food-deprived beetle larva to one plastic container under the same conditions, but without any tadpoles. Treatments and control experiments were run at the same time over the course of four days.

We monitored experiments and recorded data every two hours during each 12-hour period. Fourteen experiments were conducted from 12:00 am until 12:00 pm over four consecutive days (day 1 = four replicates, day 2 = three replicates, day 3 = four replicates and day 4 = three replicates), according to the number of tadpoles and beetles ready to be introduced into an experiment. We then measured mortality in tadpole survival experiments and both control treatments. Dead, but physically intact tadpoles with no signs of injury/attack were not included in the predation mortality totals. Individual beetle larvae and tadpoles were only used once.

## Statistical analyses

To estimate the overall dietary composition of *S. quinquefasciatus* in the agricultural areas of Santa Cruz, we calculated two indices for each taxon found in the stomach contents: (1) numerical percentage of each prey consumed and (2) frequency of occurrence. Numerical percentage estimates the quantity of ingested prey items by dividing the total stomach contents from a specific order by the total number of prey items (according to the method of Calver and Wooller 1982). Frequency of occurrence estimates the per-taxa breakdown within the diet by dividing the number of digestive

tracks containing a specific taxon by the number of stomachs containing food content. Frogs with empty stomachs were not included in the analysis.

Since we sampled frogs in the breeding season, we also hypothesised that the presence of prey in the stomach (vs. an empty stomach) would differ based on sex. We conducted an analysis of variance (ANOVA) to compare the amount of stomachs with prey items amongst males and females. We previously checked for homogeneity of variances amongst groups by using a Hartley's $F_{max}$ test.

To determine if the predation-related mortality in tadpoles was time-dependent, we used a Generalised Estimating Equation (GEE). The GEE tests for subject (trial number) and within-subject (time-interval) effects in a repeated-measure experimental design, considering these as random factors. In our model, the response variable was cumulative predation-related mortality, while the explanatory variable was time interval. We only counted the experimental units in which the predator remained alive until the end. After running the model, we used a post-hoc Bonferroni test ($\alpha = 0.05$) to determine which time intervals were responsible for significant differences in cumulative predation-related mortality.

We used another GEE test to determine if cumulative non-predation-related mortality was significantly different between tadpole survival (control) and predatory capacity experiments. Since mortality was not normally distributed, we chose a negative binomial distribution with a logarithmic link function for the model. Cumulative non-predation-related mortality was selected as the response variable, while experiment type (predatory capacity vs. tadpole survival) and time intervals were set as explanatory variables. Subject and within-subject effects were the same as in the previous analysis. All statistical analyses were performed with SPSS, version 22 (IBM Corp. 2013).

## Results

### Stomach-content analyses

Out of the 228 captured individuals (136 males, 79 females and 13 subadults), 54 had stomach content (34 males, 18 females–16 of which were gravid-and 2 subadults). Of those, 36 were collected from the core locality and 18 from the additional agricultural sites (Fig. 1). Five of the seven collection sites had individuals with ingested terrestrial invertebrates (Core location, B, C, D and E). Adult males were more frequently collected than either females or sub-adults. The stomachs of 5.8% of the collected specimens contained food items with a high degree of digestion, forming an amorphous substance for which identification of individual invertebrates was not possible.

The 54 specimens found in *S. quinquefasciatus* stomachs consisted mostly of Lepidopterans (numerical percentage [NP]: 30%, frequency of occurrence [FO]: 61.11%), followed by Acarina (NP: 44.38%, FO: 5.56%). In total, 160 macroinvertebrates from

**Table 1.** Description of prey items identified in *Scinax quinquefasciatus* individuals, classified by order. Total number of prey items represents the total number of individual invertebrates in each order consumed by collected frogs (multiple individuals could be found in the same stomach). Frequency of consumption represents the number of stomachs in which a specific order was found. Numerical percentage is the number of prey items (per order) divided by the total number of prey items (n = 160). Frequency of occurrence represents the number of stomachs that contained a specific taxon (frequency of consumption) divided by the total number of stomachs with food content (n = 54).

| Order | Total number of prey items | Frequency of consumption | Numerical percentage | Frequency of occurrence |
|---|---|---|---|---|
| Lepidoptera | 48 | 33 | 30 | 61.11 |
| Acarina | 71 | 3 | 44.38 | 5.56 |
| Araneae | 6 | 5 | 3.75 | 9.26 |
| Blattodea | 1 | 1 | 0.63 | 1.85 |
| Neuroptera | 2 | 2 | 1.25 | 3.70 |
| Hymenoptera | 9 | 6 | 5.63 | 11.11 |
| Orthoptera | 5 | 5 | 3.13 | 9.26 |
| Hemiptera | 2 | 2 | 1.25 | 3.70 |
| Isopoda | 9 | 2 | 5.63 | 3.70 |
| Coleoptera | 5 | 4 | 3.13 | 7.41 |
| Dyptera | 2 | 1 | 1.25 | 1.85 |

11 orders were identified as prey items (Table 1). The Hartley's $F_{max}$ test verified the assumption that variances were equal across groups. We found no significant differences in the number of stomachs with prey items between males and females (ANOVA: $F[1,8] = 0.40$, $p < 0.05$).

## Predator-prey experiments

Nine out of the fourteen predator capacity experiments were included in the final model, since we only used the trials in which the beetle predator survived the entire experiment duration (4 days). Cumulative predation-related mortality significantly decreased over time (Wald Chi-Square = 125.92, df = 5, p = 0.001, Fig. 2). The post-hoc Bonferroni test ($\alpha = 0.05$) showed that during the first two-hour interval, the number of predated tadpoles was the highest, with a mean value of 4.89 tadpoles. This was significantly different from the third-, fourth-, fifth- and sixth-time intervals (Table 2).

There was no significant difference in tadpole mortality between the non-predation deaths that occurred in the predatory capacity experiments versus those that occurred without the presence of a predator (Wald Chi-Square = 1.61, df = 1, p = 0.20, Fig. 2). Tadpole mortality was not significantly different over time (Wald Chi-Square = 5.03, df = 3, p = 0.17, Fig. 2). Only four of the tadpole control trials ended with one or two dead tadpoles; none died in the other ten experiments. Beetle larvae died before the end of the experiment in eight of the larvae control trials.

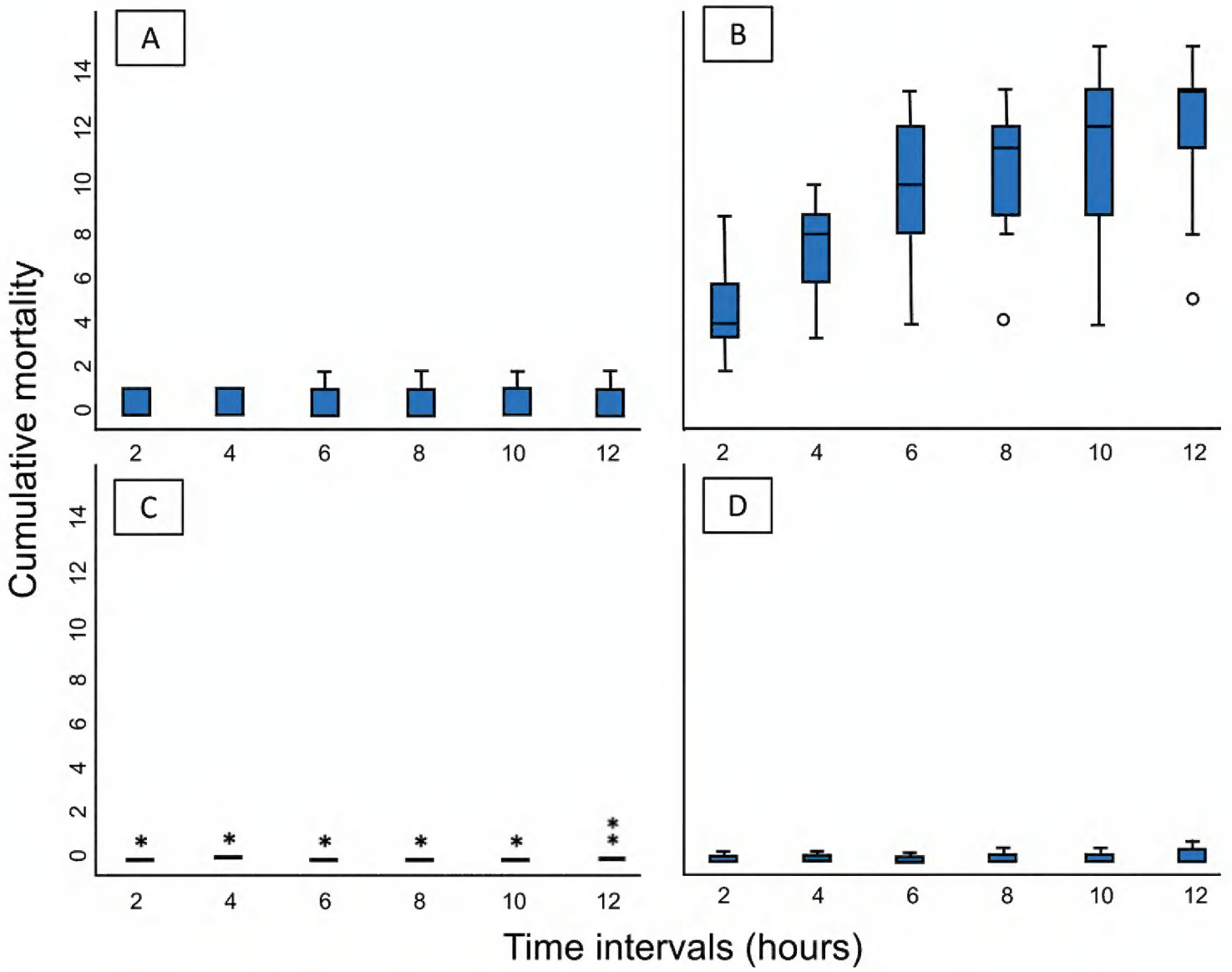


**Figure 2.** Boxplots depicting comparisons of cumulative mortality rates in predator-prey experiments over time (predator = *Thermonectus basillarus galapagoensis* larvae; prey = *Scinax quinquefasciatus* tadpoles) **A** cumulative non-predation-related mortality of tadpoles in predatory capacity experiments **B** cumulative predation-related mortality of tadpoles in predatory capacity experiments **C** cumulative larvae mortality in survival control experiments **D** cumulative non-predation-related mortality in tadpole survival experiments. Empty circles outside boxplots represent outlier values (1.5 times higher than box height). Asterisks represent extreme outlier values (3 times higher than box height).

## Discussion

One way to determine the trophic effect of an introduced species is to carry out a stomach-content analysis. In this study, *Scinax quinquefasciatus* in the highlands of Santa Cruz are shown to have a diet that consists mostly of Lepidopterans, followed by Acarina (Table 1). These results are consistent with those found by Mieles (2006), who found that Lepidopterans were also one of the most common prey orders of *S. quinquefasciatus* on Isabela. However, that study did not specify the frequency of Lepidoptera consumption.

This apparent preference for Lepidopterans is likely due to their availability in the environment. Anurans are typically diet generalists (Duellman and Trueb 1994), which enables them to compete with native species that are likely specialised to local biotic conditions. Abiotic factors could also influence the availability of certain in-

**Table 2.** Results of the Bonferroni post-hoc test (α = 0.05), describing differences between time intervals in the cumulative number of *Scinax quinquefasciatus* tadpoles predated on by the beetle larvae *Thermonectus basillarus galapagoensis* during the execution of 12-hour predator capacity experiments (N = 9). Asterisks indicate significant differences between mean values of predated tadpoles with a 95% confidence level.

| Time intervals | Cumulative # of predated tadpoles (mean value across trials) | Difference in predated tadpoles between time intervals | | Significance |
|---|---|---|---|---|
| 1st<br>0 h – 2 h | 4.89 | 0–2 h vs. 2–4 h | -2.44 | |
| 2nd<br>2 h – 4 h | 7.33 | 0–2 h vs. 4–6 h | -4.89 | * |
| 3rd<br>4 h – 6 h | 9.78 | 0–2 h vs. 6–8 h | -5.11 | * |
| 4th<br>6 h – 8 h | 10 | 0–2 h vs. 8–10 h | -6 | * |
| 5th<br>8 h – 10 h | 10.89 | 0–2 h vs. 10–12 h | -6.67 | * |
| 6th<br>10 h – 12 h | 11.56 | | | |

sects. In the highlands of Santa Cruz, various sources of artificial light (i.e. street lighting or home-generated light) attract a significant number of nocturnal Lepidopterans (Rydell 1992; Hölker et al. 2010), facilitating their predation (Rydell 1992; Tihelka 2019). In addition, the presence of rainwater repositories for irrigation purposes serve as an egg repository for many Lepidopteran insects (e.g. Noctuidae), thus supplying additional resources for their biological development (Roque-Albelo 2006). Since community compositions of terrestrial invertebrates vary across the Galápagos Islands (Peck 2001), we expected that results from the stomach analysis in our study would be different from those obtained on Isabela (Mieles 2006). However, despite presumed differences in the diets of *S. quinquefasciatus* on the two islands, this was shown to not be the case.

Sex did not influence the likelihood that a frog's stomach contained prey: 22.8% of females and 25% of males had prey items in their stomachs. This may be related to the fact that we sampled during the *S. quinquefasciatus* mating season (rainy season, December-May), when both sexes are expending energy on breeding. In many frog species, males invest more energy in behaviour related to reproduction than foraging during the breeding period (Wells 1978; Given 1988). The abundance of prey items in this anthropogenic system may mitigate the trade-off between eating and reproducing.

Even though most studies on introduced species focus on their effect on native prey communities (Fritts and Rodda 1998; Ricciardi and Cohen 2007), their role as prey is equally important. This study provides the first record of a *S. quinquefasciatus* predator in Galápagos: the endemic diving beetle *Thermonectus basillarus galapagoensis*. Our controlled predator-prey experiments indicated that the beetle larvae had a significant influence on the mortality rates of *S. quinquefasciatus* tadpoles. Studies in other ecosystems have also provided evidence of tadpole vulnerability to aquatic beetle

predators (i.e. Formanowicz 1986; Müller and Brucker 2015), but this is the first account for the Galápagos Archipelago.

If the feeding behaviour of *T. b. galapagoensis* larvae were selective (i.e. showing a strong preference for tadpoles) and/or if their populations were highly abundant, this endemic beetle could serve as a biological control for *S. quinquefasciatus*. However, our predator-prey experiments showed that the endemic beetle larvae stopped feeding before the tadpole resource was depleted, predating on a total mean value of 11.6 tadpoles after the 12-hour period. This 'feeding saturation' has direct implications for *S. quinquefasciatus* population control, suggesting that the predator-to-prey ratio is too skewed for the beetle to diminish populations of the invasive frog. This mirrors our observations in nature: there were far more tadpoles than beetle larvae in each surveyed water body on Santa Cruz. *T. b. galapagoensis* larvae presumably preyed on other animals prior to the arrival of *S. quinquefasciatus* to the island, but our finding also suggests that the beetle larvae have not developed a tadpole specialisation-decreasing its potential as a natural control agent. A recent study showed that an introduced bird, the smooth-billed ani (*Crotophaga ani*), feeds on *S. quinquefasciatus* adults in Galápagos, but predation rates are also too low to have an effect on the frog's population size (Cooke et al. 2020).

Population dynamics of introduced and invasive species depend on biological parameters (e.g. fecundity, growth, survival; Nakano et al. 2015)–and in this particular case, water reservoirs, prey availability and the expansion of agricultural sites. Our results suggest that *S. quinquefasciatus* populations are likely to remain stable or even increase on Santa Cruz. Their main prey items are common (Peck 2001) and, although tadpole predation occurs, it is currently not sufficient to decimate local populations. Additionally, the increasing occurrences of artificial ponds and rainwater reservoirs in the agricultural areas of Santa Cruz provide ideal habitats for reproduction and hydration-necessary components for anuran survival and growth (Rogowitz et al. 1999; Brand and Snodgrass 2010). As agricultural expansion continues in the highlands of Santa Cruz, the reproduction and proliferation of *S. quinquefasciatus* will likely follow suit.

## Conclusion and future directions

Due to rapid development and the increasing human population, Santa Cruz is prone to invasive species events. *Scinax quinquefasciatus* is the first successfully invasive amphibian on the island; furthering our understanding of its ecological effect(s) is crucial for management, especially in such a fragile and unique ecosystem. As reproduction for both frogs and beetles in the highlands is apparently restricted to water sources provided in the rainy season and/or anthropogenic structures, we recommend that long- term research be conducted to investigate the frog's ontogeny, especially in relation to beetle presence/absence.

This diet composition study was limited to higher taxonomic identification levels due to the nature of digested stomach contents (exoskeletons, wings etc.) and economic constraints that prevented us from testing with molecular methods. Further research

should address the selection of native, endemic and introduced prey item ratios using DNA-metabarcoding approaches.

Our findings strongly suggest that *Scinax quinquefasciatus* population growth is likely to remain stable or increase on Santa Cruz. The dietary preferences and predation rates by natural predators on this introduced frog should be taken into account when considering management strategies in the Galápagos Islands.

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## Supplementary material 1

**Prey orders consumed by collected Scinax quinquefasciatus in the highlands of Santa Cruz island, Galápagos, Ecuador**

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Data type: Table

Explanation note: Description of prey items identified in *Scinax quinquefasciatus* individuals, classified by order. Total number of prey items (n = 160) and total number of stomachs with food content (n = 54).

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